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DENDROGASTER (CRUSTACEA: ASCOTHORACIDA) FROM CALIFORNIA: SEA-STAR PARASITES COLLECTED BY THE *ALBATROSS*

By

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ABSTRACT: Californian specimens of the ascothoracid crustacean genus *Dendrogaster*, discovered by W. K. Fisher in sea-stars collected by the ALBATROSS, are reviewed. *Dendrogaster arbusculus* Fisher, represented by a female and nauplii from *Hippasteria californica* Fisher, is redescribed, with special attention to the female internal anatomy. Also, two new species are described: *D. fisheri* n.sp., represented by two females, from *Pedicellaster magister megalabis* Fisher; and *D. punctata*, represented by females, a male, metanauplii, and ascothoracid larvae, from *Poraniopsis inflata* (Fisher). These are the only ascothoracids so far described from the west coast of the Americas south of Alaska.

Introduction

Ascothoracida Lacaze-Duthiers, 1880, is often classified (under the name Ascothoracica Gruvel, 1905) as a primitive order of Cirripedia (e.g., Lacaze-Duthiers 1880, 1883; Knipowitsch 1892; Gruvel 1905; Newman et al. 1969), but arguments for its elevation to an independent subclass have also been made (Wagin 1937, 1947, 1976; Grygier 1980b, 1981a). The taxon now comprises about 40 species in 10 genera, all parasites of echinoderms or coelenterates (reviewed by Wagin 1976).

Dendrogaster Knipowitsch, 1890, parasitic in the coelomic cavity of sea-stars (Asteroidea), is the largest genus in the subclass. It includes over 20 species about the world, the taxonomy and biology of which have been studied principally by the Russian worker Wagin (especially 1950, 1954, 1957; summarized 1976). Other workers on this genus have included Knipowitsch (1890, 1891, 1892), Le Roi (1905, 1907), Okada (1925, 1938, 1941), Yosii (1931), Korschelt (1933), Hickman (1959), Achituv (1971), Karande and Oguro (1979, 1981a, 1981b), and Grygier (1981a, 1981b).

Females of *Dendrogaster* have a large, branched mantle (modified carapace) containing gut diverticula, gonads, and a spacious brood chamber. The main body is reduced, only the first antennae and mouth parts being strongly developed. Eggs hatch as nauplii, metanauplii, or bivalved ascothoracid larvae (Wagin 1948, 1954). Larvae remain within the brood chamber until the ascothoracid stage. Males, which also live in the brood chamber, have an ascothoracid larvalike main body with five pairs of natatory appendages and a muscular abdomen terminating in a furca. Their carapace lining is expanded posteriorly into a pair of winglike protrusions containing testes and a branch of the gut (Wagin 1946, 1954).

Dendrogaster arbusculus Fisher, 1911, para-

sitic in *Hippasteria californica* Fisher, 1905, is the only named ascothoracid from the west coast of the Americas outside Alaska, although I have seen a specimen of *Ascothorax* Djakonov, 1914, from Monterey Bay, and there are two undescribed species of *Dendrogaster* in the Puget Sound region (P. Illg, Univ. of Washington, personal communication). *Dendrogaster arbusculus* is incompletely known; the original description (Fisher 1911) consisted only of the locality of collection, the host sea-star, and a drawing of the holotype in situ. Yosii (1931) presented a schematic diagram of the mantle branching pattern based on Fisher's drawing. This species was included in the genus *Myriocladus* Okada, 1925 (Okada 1925; Yosii 1931; Krüger 1940), which was later synonymized with *Dendrogaster* (Wagin 1950; Hickman 1959).

Fisher (1911, 1928) found two other California sea-stars infested by *Dendrogaster*, *Poraniopsis inflata* (Fisher), 1906, and *Pedicellaster magister megalabis* Fisher, 1928, but he only specified their collection localities. His tentative identification of these parasites as *D. arbusculus* was never confirmed and, as shown below, was mistaken.

Methods and Materials

All of Fisher's finds were from sea-stars collected by the U.S. Bureau of Fisheries vessel Albatross off California in 1904; station data are listed below.

Specimen 1, holotype of *Dendrogaster arbusculus*; 5.4 km SSE of Gull Islet, off SE coast of Santa Cruz Island, 1220 m, Albatross sta. 4429, 14:IV:04; host species *Hippasteria californica* (Fisher 1911:237, 404, pl. 111).

Specimen 2, holotype of *Dendrogaster punctata*; 9.9 km NW of Pt. Pinos Lighthouse, Monterey Bay, 118–554 m, Albatross sta. 4471, 14:V:04; host species *Poraniopsis inflata* (Fisher 1911:264).

Specimen 3, paratype fragments of *Dendrogaster punctata*; same station as holotype.

Specimen 4, holotype of *Dendrogaster fisheri*; 25.2 km SSW of Pt. Loma Lighthouse, San Diego, 940–960 m, Albatross sta. 4334, 14:IV:04; host species *Pedicellaster magister megalabis* (Fisher 1928:66).

Specimen 5, paratype of *Dendrogaster fisheri*; 7.4 km SW of Pt. San Pedro, Santa Cruz Island, 817–932 m, Albatross sta. 4427, 9:III:04; host species *Pedicellaster magister megalabis* (Fisher 1928:66).

Dendrogaster-infested sea-stars or isolated specimens of the parasites were obtained from the California Academy of Sciences (CAS) and the National Museum of Natural History (USNM). In cases where a sea-star still contained its parasites, the host was dissected and the specimen of *Dendrogaster* removed. One previously isolated but dried-out mantle fragment was reconditioned in a 10% trisodium phosphate solution overnight.

At least one female of each species was dissected to remove appendages and, in the case of the holotype of *D. arbusculus*, the internal organs. Incisions were made sparingly in each female in a search for males and larvae. A male and several larvae from the species parasitic in *Poraniopsis inflata*, as well as several larvae from *D. arbusculus*, were examined whole in lactic acid; some larvae of each species were dissected. Permanent mounts were made in Turtox CMC-10 with acid fuchsin or in glycerine jelly. Drawings were done with the aid of a camera lucida.

Systematic Section

Ascothoracida Lacaze-Duthiers, 1880

Dendrogastridae Gruvel, 1905

Dendrogaster Knipowitsch, 1890

Dendrogaster arbusculus Fisher, 1911

(Figures 1 & 2)

Myriocladus arbusculus: Okada 1925:371.

Material.—One female, holotype, deposited as CAS 013159.

Diagnosis.—Female large. Middle piece four times as long as main branches; small "extra branch" opposite middle piece. Six complexly ramifying major branches, including four posterior secondary branches and both anterior primary branches. Terminal protuberances conical, scattered. Third article of first antenna with fusion seam, proximodorsal muscle, and dorsal seta. Nauplii about 1 mm long, with setose appendages. Males and ascothoracid larvae unknown.

Description of Female.—General appearance. Fisher's illustration of the holotype of *D. arbusculus* (1911:pl. 111, fig. 1) accurately portrays the parasite and its position within its host. The mantle is a whitish branched sac extending

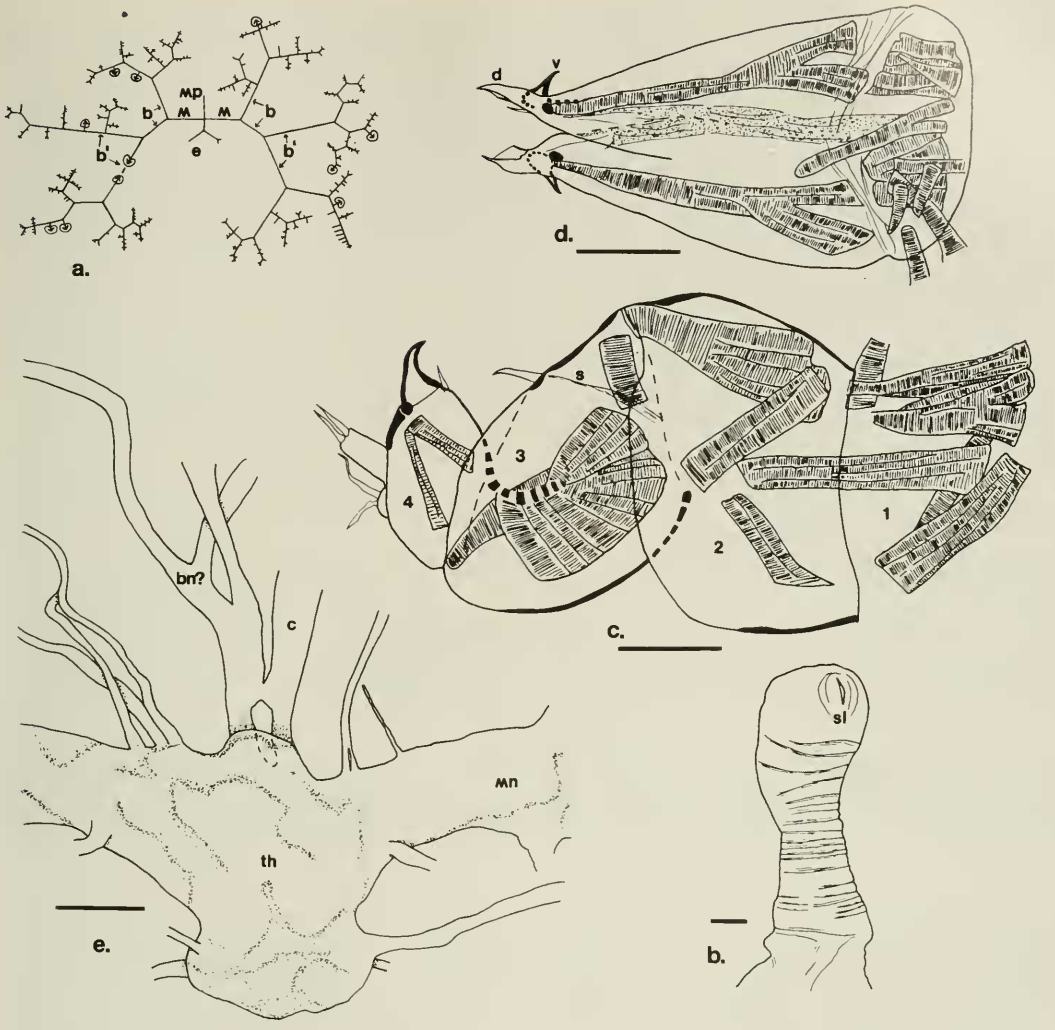

FIGURE 1. *Dendrogaster arbusculus* Fisher; holotype, female. (*a*) Schematic diagram of mantle branching pattern, terminal protuberances omitted, encircled arrows representing broken ends, opposed arrows (lower left) indicating reconstruction (orientation of distal part arbitrary). (*b*) Middle piece, dorsal view. (*c*) First antenna with musculature, articles numbered. (*d*) Second maxillae with musculature, anterior view. (*e*) Thoracic part of nervous system, dorsal view. Explanation: b, primary branches; b', secondary branches; bn?, buccal nerve?; c, circumesophageal connectives; d, distal prong; e, "extra" branch; m, main branches; mp, middle piece; s, fusion seam; sl, distal slit; th, thoracic nerve mass; v, ventral prong. Scale bars 0.1 mm, except 1.0 mm in *b*.

about 50 mm in the preserved state. The branches are constricted at nodes and expanded elsewhere, especially distally. The very thin outer cuticle of the mantle covers a loose network of longitudinal and circular muscle fibers. The focal point of the branching pattern (Fig. 1*a*) is a clavate medial protuberance (middle piece) about 10 mm long with a vertical distal slit (Fig. 1*b*). The musculature of the middle piece is better developed than that of the rest of the mantle; prominent circular muscles overlie longitudinal muscular sheets.

Branching pattern (Fig. 1*a*). The descriptive terminology of the branching pattern is modified from that of Wagin (1950, 1976). A pair of laterally directed main branches arise at the base

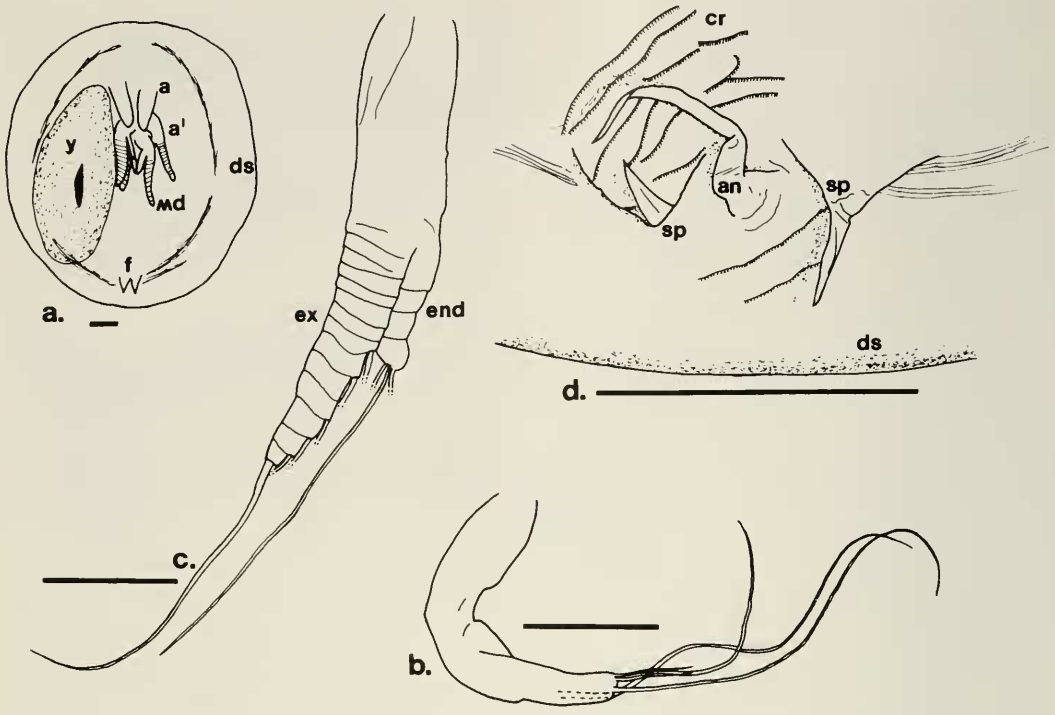

FIGURE 2. *Dendrogaster arbusculus* Fisher; nauplii. (*a*) Nauplius, ventral view, diagrammatic. (*b*) First antenna. (*c*) Second antenna. (*d*) Posterior end including furcal rudiments. Explanation: a, first antenna; a', second antenna; an, anal spine or seta; cr, ctenate ridges; ds, dorsal shield; end, endopod; ex, exopod; f, furca; md, mandible; sp, furcal spines; y, yolk. Scale bars 0.1 mm.

of the middle piece, each about 2.5 mm long. Opposite the middle piece is a short, bifurcate "extra branch." The main branches split into anterior and posterior primary branches, the latter quickly dividing into a pair of large secondary branches on each side. Further ramifications of these six major branches occur by an irregular series of bifurcations and lateral branchings, leading finally to conical terminal protuberances sometimes arranged in loose trefoils.

Internal structure of mantle. The main body, located within the slit at the distal end of the middle piece, is fused to the mantle dorsally and laterally. The subchelate first antennae and piercing-and-sucking oral cone are directed anteriorly. The thorax and abdomen are almost completely reduced, forming a sac around the gut and nervous mass. A pair of large, diaphanous gut diverticula pass posteriorly along the inside of the middle piece, extend into the main branches, and follow the branching of the mantle exactly. The ovaries, attached all along the gut diverticula, are tissue strands or tubules, the lateral follicles of which each contain a developing oocyte (cf. Okada 1941, for description of similar arrangement in another species). The mantle cavity is a brood chamber for eggs and nauplii.

First antennae (Fig. 1*c*). The first antennae are four-segmented and subchelate, 0.7 mm long. The shape of the first article could not be determined; its musculature consists of two dorsal flexors and two ventral extensors of the second article and a long flexor inserted on the proximoventral corner of the third article. The second article is rectangular. A flexor and an extensor muscle run from its proximodorsal corner to the proximal corners of the third article; another flexor runs from its proximoventral side to the proximoventral corner of the third article. The third article is subrectangular, with its distal edge facing somewhat dorsally. A seam indicating the fusion of two articles cuts across the

proximodorsal corner; there is a seta near the distal end of the seam and a muscle within the corner set off by it. The fourth article is oval, fitting lengthwise into the distal end of the third. There are two anterior processes, the first a small mound with two setae, the other cylindrical with two setae on the right first antenna, three on the left. There is a seta at the base of the heavy distal claw. Two claw-retracting muscles run from a thickening anterior to the claw (cf. Grygier 1981b); one attaches to the side of the article, the other to its basal apodeme. This apodeme extends far into the third article; a very powerful fan of flexor muscles reaches from it to the ventral and proximal sides of that article. A less powerful extensor muscle runs alongside the flexors from the ventral base of the fourth article to the proximal end of the third.

Oral cone. The oral cone is directed anteriorly. The labrum forming the sheath of the cone is drawn out laterally and ventrally, almost enclosing the mouth parts. The basal part is swollen with the insertions of the buccal pump muscles. The only mouth parts are the harpoon-shaped second maxillae (Fig. 1*d*), which protrude from the cone. They are fused for half their length. The distal prong at the tip of each consists of a thick point and a membranous flange. The ventral hook is bent laterally downwards and is more heavily chitinized than the distal prong. A muscle runs from its base to the base of the mouth part, where it ends at a transverse wrinkle indicating an articulation. There are many short muscles more proximally.

Internal anatomy. The buccal pump is a mass of circular, longitudinal, and radial muscles occupying the bulk of the oral cone. It encloses the chitin-lined esophagus which leads into the midgut, from which the digestive diverticula emerge. In other species of *Dendrogaster*, the gut is blind (Knipowitsch 1892; Le Roi 1907; Okada 1925; Wagin 1954); it was not possible to confirm that this is the case here.

The nervous system (Fig. 1*e*) is highly concentrated in the thorax. A pair of round, medially connected cerebral ganglia lie anterior to the esophagus; though they are said to give off large antennular nerves (Wagin 1954), these were not found. Lateral connectives from the cerebral ganglia pass around the esophagus, giving off a pair of bifurcate buccal (?) nerves. The connectives are linked by a commissure before they enter the anteroventral part of the thoracic nerve mass. From this mass, which is not divided into ganglia, a pair of very large nerves arise laterally to innervate the mantle. Several small nerves arise on each side near their bases, two or three anteriorly and one posterodorsally. Two pairs of fairly large nerves arise laterally from the posterior end of the thoracic mass, one dorsal and one ventral. It is impossible to say what structures all these nerves innervate; no such proliferation of nerves has been described in *Dendrogaster* previously (cf. Wagin 1954).

A pair of large, wrinkled saclike organs were removed with the second maxillae. These may be the maxillary glands, though no ducts could be followed nor openings on the maxillae located.

A cavity within the main body contained a white, friable substance which resembled yolk except for its color. A similar organ has been described in a new Antarctic species of *Dendrogaster*, where it was considered a vitellogenous organ (Grygier 1981b; also see Grygier 1980a). It more likely represents the proximal part of the oviduct.

Gametes and Larvae.—Eggs. Hundreds of eggs were found within the mantle cavity. They are yellow and subspherical, averaging 0.51 mm × 0.45 mm.

Sperm. Patches of sperm cells are attached to membranes within the mantle. Their heads are about 4.2 μm long, 1.7–2.0 μm wide, tapered slightly anteriorly, with a small terminal acrosome. The midpiece is granular and tapers posteriorly for about 6.4 μm. The tail is at least 20.4 μm long and probably much longer. These sperm are similar to those of other species of *Dendrogaster* studied by light microscopy (Le Roi 1907; Okada 1941) and by electron microscopy (Grygier 1981a). If these sperm are not autochthonous but are actually ingested starfish sperm, they should have round heads (Dan 1968), not the observed oblong heads.

Males.—It is puzzling that no males were found in this female. Nauplii occupied the brood chamber; therefore, fertilization must have taken place. Parthenogenesis has been suggested in *D. murmanensis* Wagin, 1950 (Kluge, unpublished data cited by Wagin 1947), and *D. repertus* Le Roi, nom. nud. (Le Roi, unpublished data cited by Krüger 1920), but since sperm were

present, it is unlikely to have been the case here. One possible case of hermaphroditism is reported. Okada (1941) found that the anterior region of the ovary in *D. okadai* (Yosii, 1931) produced spermlike cells rather than ova. He did not explain why he did not consider these true sperm. No obvious testes were found in the present specimen, but internal investigations were minimized to preserve the integrity of the holotype. It is also possible that a dwarf male was lost when the mantle was damaged upon removal from the host.

Nauplii (Fig. 2).—About 24 nauplii, each about 1.0 mm long and 0.9 mm wide, were found (Fig. 2*a*). The dorsal shield is bowl-shaped, oval in dorsal view, with a broad rim. The main body of the nauplius completely fills the bowl's concavity. It has three pairs of naupliar appendages, a simple labrum, and a rudimentary furca, but no nauplius eye. The first antennae are uniramous and unsegmented, and have three long and two short distal setae (Fig. 2*b*). The second antennae and mandibles are alike (Fig. 2*c*), with an obscurely divided protopod, an exopod formed of about 13 annuli, the last 6 or so each bearing a long seta, and an endopod half as long as the exopod with about four indistinct articles and three setae. The labrum is small, its posterior margin acute. The furca (Fig. 2*d*) consists of a pair of conical mounds, each with a spine at the apex. A long, flexible anal spine arises between and dorsal to them. Between the labrum and furca, more pronounced along the midline and posteriorly, are a number of ctenate cuticular ridges.

Affinities.—The elucidation of interspecific relationships among the species of *Dendrogaster* has so far proved intractable. Okada's (1925) segregation of several species (including *D. arbusculus*) into a new genus, *Myriocladus*, is no longer accepted. Provisional attempts to correlate morphology of the parasites with the phylogeny of their host sea-stars have been unsatisfactory (Yosii 1931; Grygier 1981b).

Wagin (1976) proposed another approach based on his investigations (Wagin 1947, 1948, 1954) of embryonic and larval development in ascothoracids, including species of *Dendrogaster*. He distinguished three kinds of larval development in this genus. *Dendrogaster astropectinis* (Yosii, 1931) and *D. beringensis* Wagin, 1957, hatch from the eggshell as nauplii. Other species hatch as metanauplii, and yet others as ascothoracid larvae. Wagin considered the first variation the most primitive and suggested that the deep bathyal habitat (2000–4000 m) of the two species exhibiting it was the critical factor in its retention. *Dendrogaster arbusculus* hatches as a nauplius that is more perfectly formed than that of *D. astropectinis*, and the present specimen was captured at shallow bathyal depths (1200 m). These facts may not indicate affinities between *D. arbusculus* and either *D. astropectinis* or *D. beringensis*, however, because the presence of a free naupliar stage is a plesiomorphic feature.

Neither of the other two species remotely resembles *D. arbusculus* in its branching patterns. Like *D. arbusculus*, females of *D. astropectinis* have a fusion seam and a proximodorsal muscle in the third article of the first antenna. This conformation, which is also plesiomorphic, is not limited to these two species, however, being found also in *D. iwanowi* Wagin, 1950, *D. tasmaniensis* Hickman, 1959, and both new species described below. The occurrence of a single seta on this article is limited to *D. arbusculus* and one of the new species below. *Dendrogaster ludwigi* Le Roi, 1905, and *D. dogieli* Wagin, 1950, the only other species in the genus with an "extra branch" like *D. arbusculus*, otherwise have unique branching patterns not resembling that of the present species.

Dendrogaster fisheri, new species
(Figure 3)

Dendrogaster cf. *arbusculus:* Fisher 1928:66.

Material.—Two females. Holotype from Albatross sta. 4334 deposited as USNM 184574; paratype from Albatross sta. 4427 as USNM 184575. Holotype occupied four arms of host, middle piece directed outward in interradius (Fig. 3*a*); paratype occupied only two arms of host.

Diagnosis.—Females small to medium-sized, with four equally developed primary branches. Short middle piece more than twice as long as main branches; short, lobate secondary branches arising alternately from primary branches. Third article of first antenna with fusion seam, proximodorsal muscle, and two or three dorsal setae, one removed from rest. Males, nauplii, and ascothoracid larvae unknown.

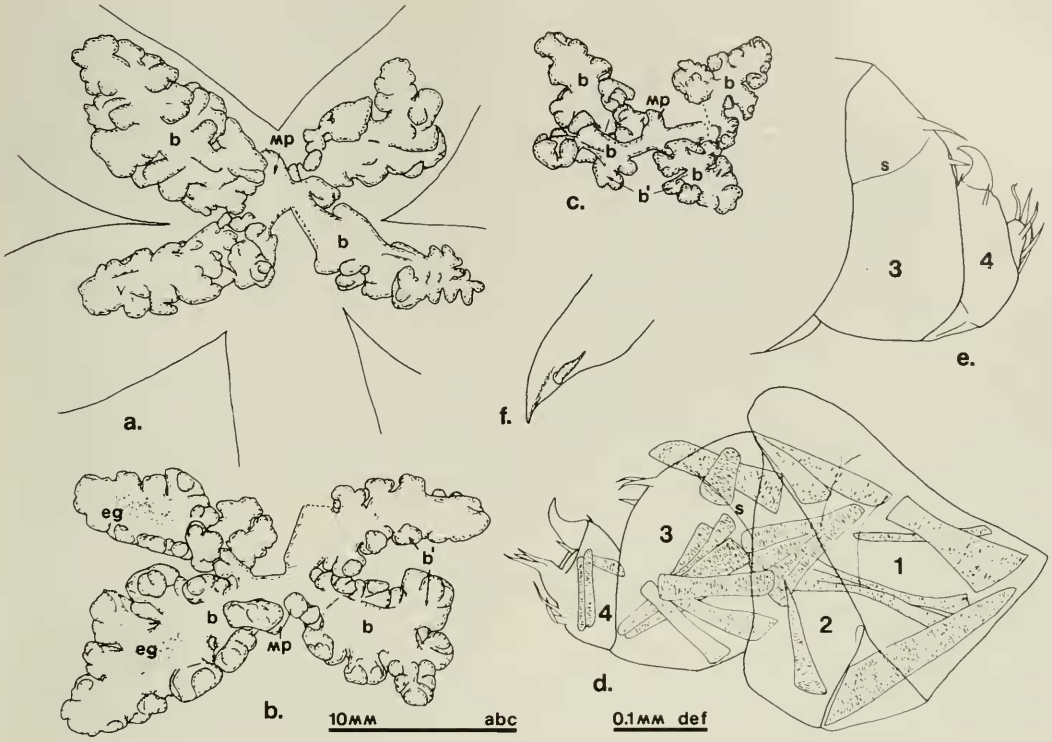

FIGURE 3. *Dendrogaster fisheri*, new species; female. (*a*) Holotype in situ in host sea-star *Pedicellaster magister megalabis* Fisher, dorsal view. (*b*) Holotype, ventral view. (*c*) Paratype, ventral view. (*d*) First antenna of paratype with musculature, articles numbered. (*e*) First antenna of holotype, distal articles (numbered). (*f*) Tip of second maxilla, lateral view. Explanation: b, primary branches; b′, secondary branches; eg, eggs; mp, middle piece; s, fusion seam.

DESCRIPTION.—General appearance. *Dendrogaster fisheri* is of small to medium size, the greatest extent of the branches being 26 mm in the holotype (Fig. 3*a*, *b*) and 14 mm in the paratype (Fig. 3*c*). The mantle surface is smooth with clearly visible longitudinal muscles. Its color in the preserved state is pale brown to pale yellow. The oral cone and left first antenna of the holotype protruded through the distal slit of the middle piece before dissection, but no part of the paratype's main body was visible externally.

Branching pattern. The middle piece of the holotype is 2 mm long, bluntly conical with a distal slit. The main branches are very short (less than 1 mm), each dividing into a pair of primary branches 9–12 mm long in the holotype, 6–9 mm long in the paratype. The anterior and posterior primary branches are equally developed. Many short secondary branches arise alternately from the anterior and posterior sides of the primary branches, the proximal ones slightly larger than the distal ones, each bearing several blunt terminal protuberances.

First antennae (Fig. 3*d*, *e*). The four-segmented, subchelate first antennae are massive, 0.5 mm long in the paratype (Fig. 3*d*), larger in the holotype (Fig. 3*e*). The basal article is triangular, attached to the head by its longest side, and with its sharpest apex uppermost; it contains the flexor and extensor muscles of the second article and a flexor muscle of the third article. The second article is rectangular, smaller and shorter than the first, and contains flexor and extensor muscles of the third article. The third article is an irregular quadrilateral higher than long, with a fusion seam across its proximodorsal corner and two or three dorsal setae

distal to the seam (one isolated far distally); it contains flexor and extensor muscles of the fourth article and an isolated muscle in the corner delimited by the fusion seam. The fourth, distalmost article is short, almost square, with a distal claw and two claw retractor muscles. It is armed with a small seta lateral to the claw, a process on the distal face with three setae, and a small seta at the base of the claw.

Oral cone. The only obvious mouth parts, the second maxillae, are enclosed in a sheathlike oral cone formed from the labrum. The tips of the second maxillae are bifurcate (Fig. 3*f*); the ventral hook can be bent laterally and posteriorly with respect to the distal prong. The tips are directed away from each other when the mouth parts protrude from the oral cone.

Gametes and Larvae.—In both specimens a large number of eggs about 0.5 mm in diameter distend the primary branches and bend the secondary branches ventrally (Fig. 3*b*). No dwarf males or larvae were found in a cursory search of both specimens.

Affinities.—Fisher (1928) tentatively assigned these specimens to *D. arbusculus*. There is no real similarity, however, since *D. fisheri* has only four major branches with no complicated higher-order branching, a relatively shorter middle piece than *D. arbusculus*, and no "extra branch" opposite the middle piece. At the time of Fisher's publication, only four other species of *Dendrogaster* had been named and the extent of intraspecific variation of branching patterns, still incompletely known (but see Karande and Oguro 1981b), could not be estimated. Since the two available specimens of *D. fisheri* are alike in most respects, including their common host, I am proposing a new species for them. In recognition of his having informed zoologists of the existence of these specimens, I take pleasure in naming the species after W. K. Fisher.

Dendrogaster fisheri superficially resembles young specimens of *D. arctica* Korschelt, 1933, which also have four equal primary branches with lobular side branches (Wagin 1950), but in *D. arctica* the secondary branches are simple, lacking terminal protuberances. The first antenna has no fusion seam or associated muscle, only two setae on the third article, and a single seta proximal to the process on the fourth article (Wagin 1950). *Dendrogaster arctica* inhabits the Bering Sea (Fisher 1930; Wagin 1950) and Hudson Bay (undocumented record on distribution map by Wagin 1970), and parasitizes the sea-star *Leptasterias groenlandica* (Lütken), 1857.

Dendrogaster ludwigi also has four primary branches. The secondary branches, though short, are so densely covered with terminal protuberances that the primary branches are completely obscured, whereas in *D. fisheri* the primary branches are easily discernible. *Dendrogaster ludwigi* lives in shallow water from Japan to Australia (Le Roi 1905, 1907; Yosii 1931; Kenny 1959); its range is unlikely to extend to the east Pacific, especially in waters as deep as *D. fisheri*'s habitat (800–1000 m).

In no other known species of *Dendrogaster* is the mantle constructed around four relatively simple primary branches.

Dendrogaster punctata, new species

(Figure 4)

Dendrogaster cf. *arbusculus:* Fisher 1911:264.

Material.—One female, holotype, deposited as USNM 184573; several mantle fragments from same host, paratype lot, deposited as CAS 018895.

Diagnosis.—Females medium-sized with complexly branched mantle. Short, cylindrical middle piece little longer than main branches. Primary and secondary branches dichotomous, better developed posteriorly; more distal branches either unbranched and elongate or variously branched, ending in trefoil-shaped clusters of terminal protuberances. Mantle extensively pitted. Third article of first antenna with weak fusion seam, proximodorsal muscle, and dorsal seta. Males with elongate, cylindrical posterior protrusions; testes ribbonlike. Third article of first antenna in males and ascothoracid larvae without proximodorsal muscle, but with two long, bifid setae. Anterior face of fourth article with straplike aesthetasc, seta, and process with three setae. Late metanauplii lacking antennae.

Description of Female.—General appearance (Fig. 4*a*). The mantle extends 26 mm when the branches are spread out, but in situ the branches are curled and intertwined (fixation artifact?). The mantle is beige and fairly tough in the preserved state. Its surface is uneven, pitted by irregular small depressions (Fig. 4*b*). [The

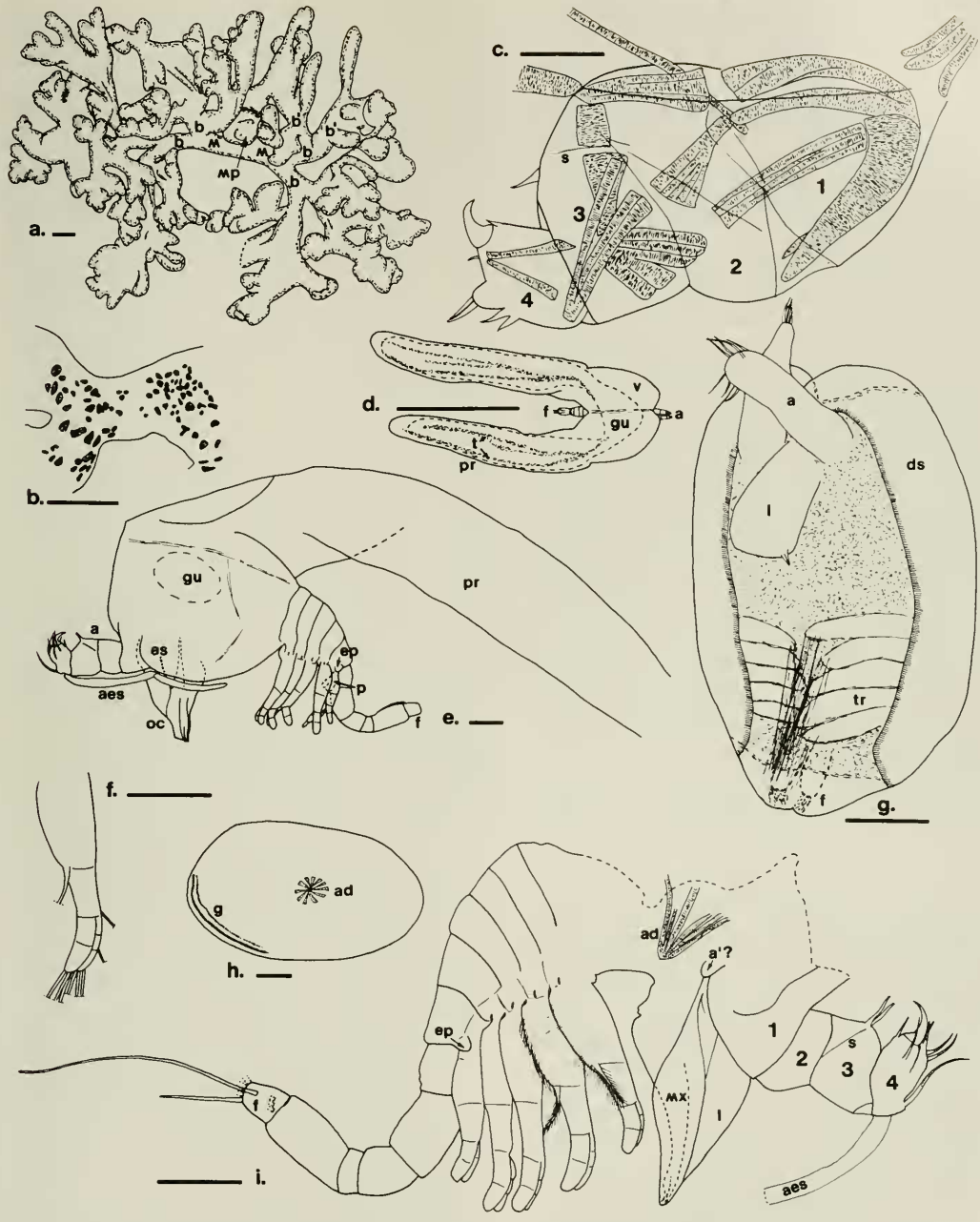

FIGURE 4. *Dendrogaster punctatus*, new species. (*a*) Holotype, female, overall view. (*b*) Detail of same showing depressions in mantle (stippled). (*c*) First antenna of same with musculature, articles numbered. (*d*) Male, dorsal view. (*e*) Male, lateral view, left valve removed, natatory setae omitted on thoracopods and furca. (*f*) Male, second thoracopod with natatory setae. (*g*) Late metanauplius, ventral view. (*h*) Carapace valve of ascothoracid larva, interior view, anterior end right. (*i*) Main body of ascothoracid larva, most thoracopod setation omitted, first antennal articles numbered. Explanation: a, first antenna; a'?, second antenna?; ad, adductor muscle; aes, aesthetasc; b, primary branches; b', secondary branches; ds, dorsal shield; ep, epaulet; es, esophagus; f, furcal rami; g, guard spinules; gu, midgut (diverticula indicated by dashed lines in *d*); l, labrum; m, main branch; mp, middle piece; mx, second maxilla; oc, oral cone; p, penis; pr, posterior protrusion; s, fusion seam; t, testes; tr, thoracopod rudiments; v, carapace valve. Scale bars 1.0 mm in *a, b, d*; otherwise 0.1 mm.

specific name is derived from this sculpturing (Latin *punctatus*: prick or point).]

Branching pattern. The middle piece is rather thick and 3.5 mm long, slightly longer than the main branches. The latter bifurcate into short primary branches, each of which bifurcates again into secondary branches, the posterior ones ramifying a little more complexly than the anterior ones. Some secondary branches bifurcate or trifurcate; others are palmate. Some tertiary branches are simple elongate lobes; usually, though, higher-order branches end in terminal protuberances arranged in trefoils.

First antennae (Fig. 4*c*). The first antennae are four-segmented and subchelate. The dorsal part of the triangular first article overlaps part of the tall, rectangular second article. The third article is a rounded quadrilateral with a faint fold indicating a fusion seam, a muscle in the corner so delimited, and one large dorsal seta. The fourth article is rhombic with a strong distal claw. Its anterior face is armed, progressively more distally, with two setae, a process with two or three terminal setae, and a smaller seta arising from the side of the article. There is a small seta near the base of the claw. The musculature is similar to that described in *D. arbusculus* and *D. fisheri*.

Oral cone. The sheath of the oral cone is formed from the expanded labrum. The mouth parts were not examined.

Description of Female Fragments.—It is not possible to determine how the several mantle fragments found together with the holotype fit together to form one or more complete specimens, especially since no middle pieces were among them. Two small fragments may be from a single specimen similar to the holotype. Two others may be from a larger specimen with fewer terminal protuberances in trefoils than the holotype and a greater proportion of unbranched, elongate higher-order branches. All fragments had pitted surfaces like the holotype.

Description of Male.—General appearance (Fig. 4*d, e*). The single dwarf male found in one of the female mantle fragments is bivalved with a cylindrical protrusion arising posteriorly from each valve. The valves are about 0.63 mm long and are held open for a total width of 0.70 mm. One posterior protrusion is 1.6 mm long, the other 1.4 mm. A midgut diverticulum partially enveloped by longitudinal strips of testicular tissue reaches nearly to the end of each protrusion (Fig. 4*d*). The main body, suspended beneath the valves, has four-segmented, subchelate first antennae, an oral cone, five thoracomeres with natatory limbs, and a five-segmented abdomen terminating in a pair of furcal rami (Fig. 4*e*).

First antennae (Fig. 4*e*). The first antennae are massive pincers protruding from the carapace. The first, triangular article is the largest; the second and third are rectangular, the latter with a proximodorsal fusion seam and a pair of large terminally bifid setae. The fourth article is smaller than the others and bears a distal claw opposing the two setae on the third article. A strap-like sensory aesthetasc almost twice as long as the first antenna arises from the ventroproximal corner. Distal to this on the anterior face is a large seta and, farther distally, a fixed process bearing three setae. Two long setae flank the claw, and a third arises at its base. All these setae narrow abruptly to a sharp point. Little can be made of the musculature, but there is no muscle in the part of the third article delimited by the fusion seam.

Oral cone (Fig. 4*e*). The oral cone is narrow. The labral margins do not meet posteriorly. The distal and posterior prongs of the second maxillae, the only mouth parts, are strongly chitinized.

Thorax. The oral cone and first pair of thoracopods are widely separated (Fig. 4*e*). A pair of ventrolateral flanges extend from the thoracopods to the first antennae, partly overlapping the oral cone. The last thoracomere has a small posterolateral epaulet (Fig. 4*e*). The thoracopods consist of a coxa, a basis, a triarticulate endopod (biarticulate in the fifth pair), and a biarticulate exopod (Fig. 4*f*). The coxae of the first two pairs each bear a large lateral seta; the first four pairs have a medial seta on the basis and their endopods have one seta on the second article and three terminal setae. All the exopods terminate in three setae.

Abdomen. There is a short, distinctly bilobed penis rudiment on the venter of the first abdominal segment (Fig. 4*e*). The furcal rami are almost square with four long medial setae, three arising basally, the fourth distally near the dorsal margin. Of the four terminal setae, the most ventral is less than half the length of the others.

Description of Larvae.—Metanauplii (Fig. 4*g*). All the mantle fragments contained numer-

ous late metanauplii about 0.55 mm long and 0.35 mm wide. The dorsal shield is folded ventrally at the sides and has a pronounced anterior indentation, presaging the bivalved carapace of the ascothoracid larva. The first antennal rudiments are cylindrical with several short terminal setae. Eyes and second antennae are lacking. A pair of stylets (second maxillae?) protrude from beneath the large labrum. No other mouth parts are visible. There are five pairs of stubby thoracopod rudiments bearing setae, as well as a pair of unerupted furcal rami with numerous short distal setae.

Ascothoracid larvae (Fig. 4*h*, *i*). These larvae are very similar to the male except that they lack posterior protrusions. The carapace valves (Fig. 4*h*) are about 0.60 mm long and 0.35 mm high. The posteroventral margin of the inner cuticle is lined with two rows of guard spinules. On the main body (Fig. 4*i*), small lobes posterior to the first antennae may be vestiges of second antennae (Okada 1938; Hickman 1959). The oral cone and thoracopods are not as far removed from each other as they are in the male, but a space remains corresponding to the lost first pair of thoracopods. The coxae of the first two pairs of developed thoracopods are armed externally with a fringe of fine hairs and a seta. Other details of setation are unclear, but are probably similar to those in the male. The main bodies of the ascothoracid larvae and males are alike in all other respects.

Affinities.—Fisher (1911) suggested that these specimens belonged to *D. arbusculus*. The complexity of the branching pattern is comparable, but numerous differences argue against this identification. The mantle of the holotype of *D. arbusculus* is much more delicate than that of *D. punctata* and lacks depressions. The middle piece is relatively much shorter in *D. punctata*, which also lacks an "extra branch" opposite the middle piece. The terminal protuberances are well expressed and rounded in *D. punctata*, but are less pronounced in the other species. The third article of the first antenna is identically armed in both species, but the two proximal setae on the fourth article are on a mound in *D. arbusculus*, not in *D. punctata*. The metanauplii and ascothoracid larvae of *D. punctata* are only about half the size of the nauplii of *D. arbusculus*.

Four other species of *Dendrogaster* have terminal protuberances arranged in trefoils. *Dendrogaster rimskykorsakowi* Wagin, 1950, is not complexly branched and the clusters of terminal protuberances are widely spaced (Wagin 1950). *Dendrogaster okadai* has oppositely pinnate higher-order branches (Yosii 1931), and *D. ludwigi* does not branch beyond the tertiary order. The new Antarctic species agrees with *D. punctata* in having several dichotomies followed by trichotomies in the higher branching orders, but it is much more robust than *D. punctata* and has very distinctive first antennae (Grygier 1980a, 1981b).

The metanauplii of *D. punctata* are peculiar in lacking rudiments of the second antennae and the first pair of thoracopods (possibly also lacking mandibles and first maxillae, but these mouth parts may be hidden under the labrum). Wagin (1954, 1976) reported the presence, albeit in reduced form, of all these appendages through the metanaupliar stages in several other species of *Dendrogaster*, although the first thoracopods were always lost in the molt to the ascothoracid larva. He may have been conservative in describing only three ontogenetic sequences among the species of this genus.

Among ascothoracid larvae and males, the long bifid setae on the third article of the first antennae are unique to *D. punctata*. In sum, this species seems to have no known close relatives elsewhere in the genus.

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